SYMBIOTIC STROMATOPOROID-NAUTILOID ASSOCIATION, MIDDLE DEVONIAN, NORTH QUEENSLAND

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The stromatoporoid *Clathrocoilona spissa* encrusts specimens of *Diademoceras* obtained from the Middle Devonian (Givetian) Papilio Mudstone, Broken River Province and Burdekin Formation, Burdekin Subprovince, north Queensland. Stromatoporoid growth commenced and flourished while nautiloids were in an upright living position. *Diademoceras*, here described for the first time in Australia, is considered upright benthonic to barely nektobenthonic. □ *Nautilida, Devonian, stromatoporoid, symbiosis, Queensland.*

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Devonian nautiloids from northeastern Australia are poorly known, despite the seminal works of Teichert (1940) and Teichert & Glenister (1952). Large and diverse faunas occur in the Burdekin Basin (Jell, pers. comm.) but are less diverse in the adjacent Broken River Province.

Five fragmentary specimens of *Diademoceras* were recovered from WSW of Storm Dam, (QML1017 and BRJ62), from the Papilio Mudstone, Broken River Province, north Queensland. Three specimens were recovered from the Burdekin Formation, Golden Valley area, near Fanning River, Burdekin Subprovince, NQ. This is the first description of *Diademoceras* from eastern Australia. *Clathrocoilona spissa* is a widespread encrusting stromatoporoid (Cook, 1994). Specimens from Papilio Mudstone were weathered from lime-mudstone units interpreted as having been deposited on a shallow-water, open marine, muddy shelf (Lang et al., 1993). The Papilio Mudstone contains an abundant fauna including corals, brachiopods, stromatoporoids and conodonts, indicative of a Givetian age (Jell et al., 1993). Material from the Burdekin Formation was retreived from carbonate mudstone and packstone units, interpreted by Cook (1995) as representing deposition on a shallow to moderately deep (5-60m) carbonate shelf within the geographically restricted Burdekin Basin. The Burdekin Formation also contains a diverse assemblage of corals, stromatoporoids, brachiopods and molluscs. Sparse conodont faunas (Talent & Mawson, 1994) also indicate a Givetian age.

STROMATOPOROID OVERGROWTHS

Five of the eight *Diademoceras* specimens possess a sheath of encrusting stromatoporoid, two others have partial encrustation and the remaining specimen has been abraded. Cut specimens show attached corals (several auloporid and rugose corals), but growth of these was dominated by that of the stromatoporoid associates. Polished blocks and thin sections were prepared to reveal growth detail of the encrusters. The stromatoporoid was identified as *Clathrocoilona spissa* (Lecompte, 1951). Each sheath consists of many growth phases of *C. spissa,* punctuated by growth inhibition and termination surfaces (*sensu* Kazmierczak, 1971). Growth was thickest on the ventral margin of the nautiloid, thinner inside its open coil. Many growth phases completely enveloped the shell indicating that development of some phases was uninhibited by the nautiloid's resting position on the substrate. These must have grown while this part of the shell was raised above the substrate. Other growth was more spasmodic. Cresentic nodes on the shell flanks of *Diademoceras* developed at the aperture. They are likely to have protected siphons for the usual paired inhalent water currents during pauses in growth but became overgrown after the shell grew further (Fig. 4c.) Thus we conclude that at times the nautiloid positioned itself upright and stromatoporoid growth commenced during the life of the nautiloid. The nautiloid, encumbered with such stromatoporoid encrustation, would have hardly been capable of significant motion in the water column, as observed by Wade (1988) who mistook poorly preserved encrusting stromatoporoid growth for part of a thick shell wall. The availability to epizoans supports the

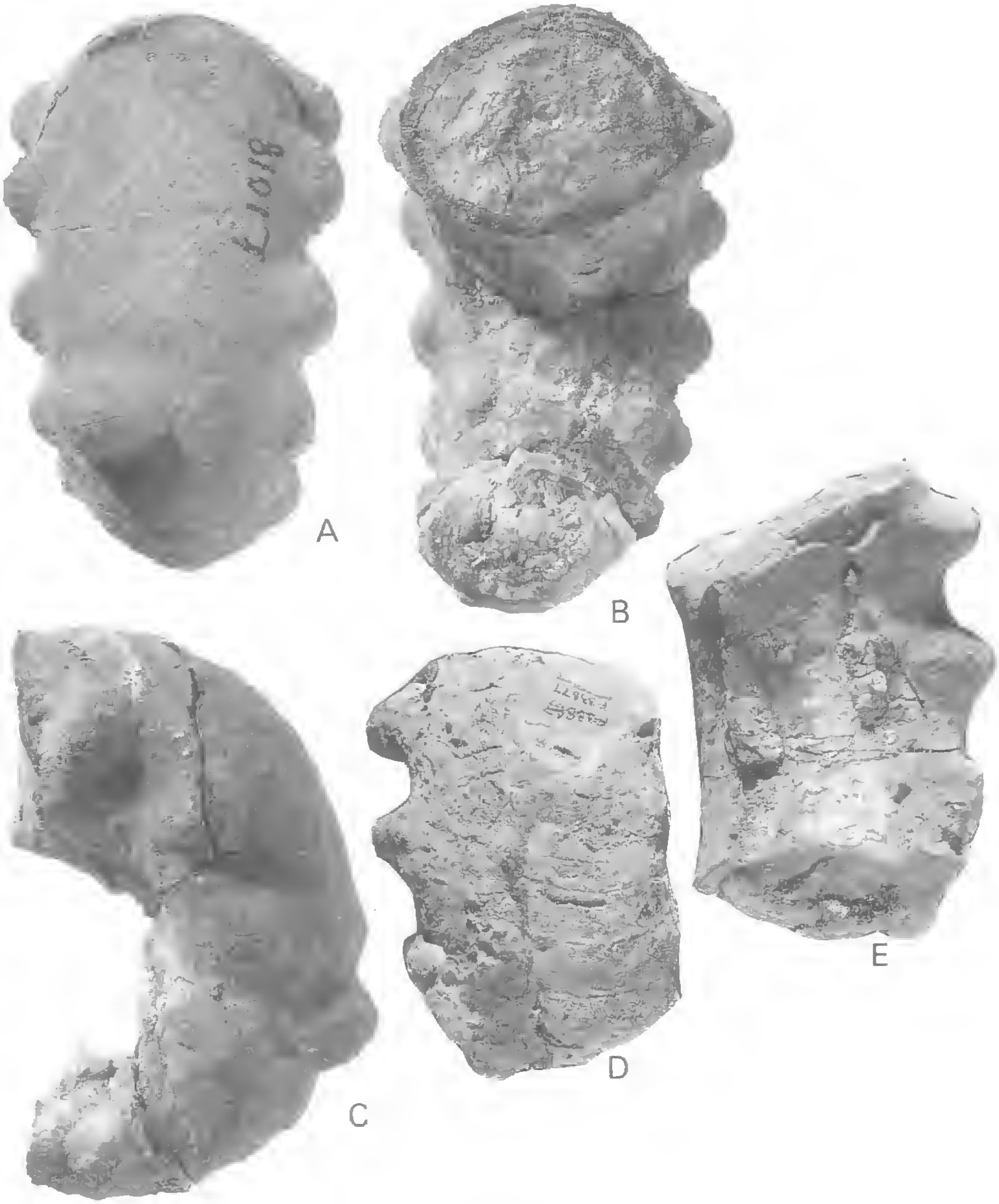

FIG. 1. *Diademoceras submammilatum* (Whiteaves) x 0.5. A-C, QMF32218, prior to sectioning. A, dorsal view; B, ventral view; C, side view. D, E, QMF33877. D, dorsal view; E, ventral view.

suggestion that the form was benthonic or barely nektobenthonic. Observed growth interruptions would have occurred through limited partial burial, shell rotation with growth or some other benthic adjustments. Some growth interruptions may be due to changes in sea-floor sedimentation effecting the vitality of the stromatoporoid. Furnish & Glenister (1964) have suggested that all

Nautilida were nektobenthonic and posthumous floaters. Considering the mass of encrusting stromatoporoid, it is unlikely that significant post mortem transport occurred here, except some by wave action.

Encrustation upon nautiloids has been reported by Teichert (1964) who stated that '*irresepective of normal bouyancy requirements such shells could not have floated appreciably after the animal died*' (Teichert,1964: K125). Frey (1988) recorded bryozoan encrustation upon *Treptoceras duseri*, a michelinoceratid from the Ordovician of Ohio. These bryozoan sheaths were uniformly thin, and Frey (1988) concluded that whilst *Treptoceras duseri* was nektonic, he could not determine whether encrustation took place during the life of the nautiloid.

SYSTEMATIC PALEONTOLOLOGY
Phylum PORIFERA Grant
Subphylum STROMATOPOROIDEA Nicholson & Murie
Order STROMATOPORELLIDA Stearn
Family STROMATOPORELLIDAE Lecompte
Clathrocoilona Lecompte 1951

Clathrocoilona spissa (Lecompte) 1951

REMARKS. Cook (1994) has described *C. spissa* from the neighbouring Burdekin Subprovince and noted its presence within Givetian strata of the Broken River Province. The material here is adequate for identification, displaying the characteristic irregular architecture, occluded irregular galleries in both tangential and vertical section, and tripartite laminae.

Phylum MOLLUSCA
Class CEPHALOPODA
Subclass NAUTILOIDEA Agassiz
Order RUTOCERATIDA Flower & Kummel

REMARKS. Nautilida are often characterised by their thin siphuncular walls, in which layering is difficult to detect (Flower, 1964), although all Nautiloidea may be observed or inferred to have had two layers applied to a basal membrane which is rarely seen in fossils (Wade, 1988). Siphuncles in the *Diademoceras* material described here are clearly layered, consisting of two thick layers and possibly one thin layer (see below).

Family RUTOCERATIDAE Hyatt, 1884

REMARKS. Most workers post-dating Flower & Kummel (1950) have agreed that Rutoceratidae, or an inclusive larger taxon, is intermediate between Oncocerida and Nautilida (Kummel, 1964). Although Teichert (1967, 1988) changed his view of the taxonomic status of Rutoceratidae as the basal family to the basal suborder of Nautilida, Flower (1964; 1988) persisted in recognising Rutoceratida between Oncocerida and Nautilida, with Rutoceratidae as the basal and nominate family. *Diademoceras*, which Flower (1949) assigned to the Rutoceratidae, has open coiling and a nodose shell, respectively rare and almost unheard of in the Oncocerida. These are rather commonplace in Nautilida. They occur here with a thick outer (supportive) layer in the connecting rings, and thin inner (osmotic pump) layer. Turek & Marek (1986) have found oncocerid muscle scars in *Ptenoceras*, assigned to Rutoceratidae, order not stated. Rutoceratidae thus appear to be 'not yet' Nautilida. The material we have is inadequate for major taxonomic revision. Faced with the choice of withdrawing a mostly unseen and inadequately described Rutoceratina to the Oncocerida or accepting Flower's original evaluation of their status, we accept his placement.

Diademoceras Flower, 1945

Diademoceras Flower, 1945: 677; Flower 1949: 74; Kummel, 1964: 418; Zhuraleva, 1974: 124.

TYPE SPECIES. *Diademoceras palmeri* Flower, 1949, by original designation from the Middle Devonian (Givetian), Cherry Valley Limestone of New York.

REMARKS. Flower (1945) erected the genus, but did not describe or figure the type material. Flower (1949) fully diagnosed and described it. He further remarked that additional taxa of *Diademoceras* were found within the Manitoban Limestone, of which *D. submammilatum* (Whiteaves) was the only described species. *?Diademoceras ajense* Zhuraleva, 1974, from the Givetian of the southern Urals, is based on fragmentary material and is poorly known. *Diademoceras ventrolobatum* Lai & Zhang, 1988 from the Middle Devonian (Givetian) Qiziqao Formation is the most recently described member of the genus.

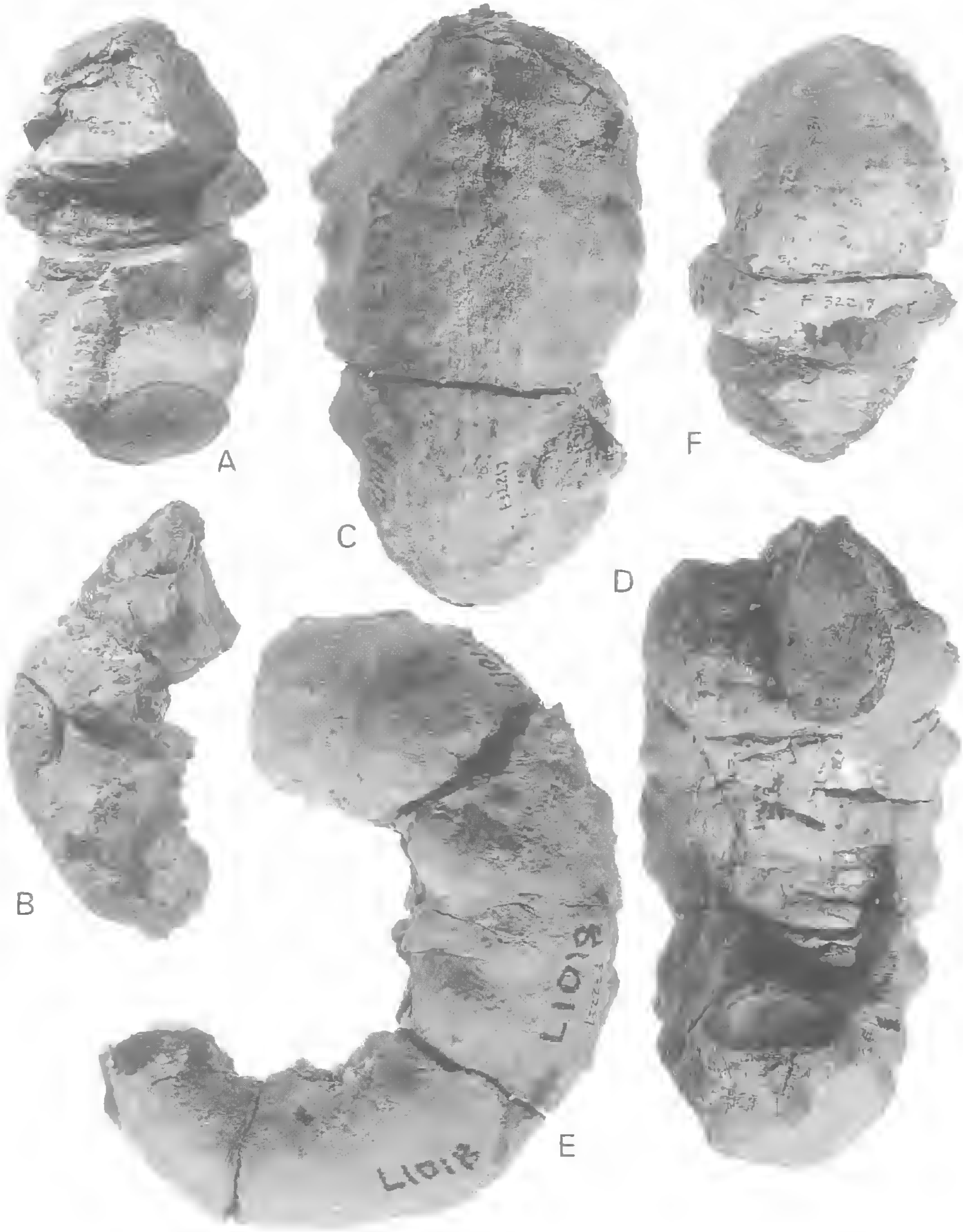

FIG. 2. *Diademoceras submammilatum* (Whiteaves) x 0.5. A,B,F, QMF32219, prior to sectioning. A, dorsal view; B, ventral view; F, side view. C-E, QMF32217. C, dorsal view; D, ventral view; E, side view.

Diademoceras submamilatum
(Whiteaves, 1891) (Figs 1-4)

Gyroceras submamillatum Whiteaves 1891: 107, pl. 10, figs. 1a,b.
Diademoceras submamillatum (Whiteaves) Flower 1949: 75.

MATERIAL EXAMINED. QMF11896, collected J. Jell, from the Papilio Formation, SW of Storm Dam; QMF32212, QMF32217-9; from QML1018, collected N. Camilleri & A. Cook, 1km S of Storm Dam, Papilio Formation, Broken River Province, north Queensland. QMF33877, QMF33879, QMF33880 collected D. Johnson & R. Henderson, from the Burdekin Formation, Golden Valley area, 'Fanning River' Station, NQ.

PRESERVATION. The nautiloid material is heavily recrystallised. Stylolites are common, and there is widespread loss of shell by solution. Septa in particular, may have been lost by aragonite solution because the calcite chamber fill is well preserved leaving adjacent crystallised chamber fills separated by thin spaces. Frequently septa are represented only by a thin, black, linear iron mineralisation. Since Allison (1988) established the sequence of early diagenetic minerals as francolite, iron sulfide, calcite, it is reasonable to trust shell-like shapes and positions of thin layers of iron mineralisation. In thin section these are represented by black lines which not only follow either surface of the septa, but may mimic septal or shell wall laminae when the original structure is lost by solution or recrystallisation. Here, as is common in open marine environments, phosphatisation was elided. Fibrous drusy calcite lined the chambers in both sectioned specimens, but this was sporadically replaced by coarsely crystalline calcite which filled the remainder of the cameral space.

Every thin section is deficient in shell material in some areas. All specimens were freed by surface weathering and have undergone some modern erosion and breakage. Some breakage presumably predates burial, since no whole whorls could be fitted together and body chambers are poorly preserved, but the original emptiness of some siphuncles and chambers is evidence against significant post-mortem movement on the sea floor although it was well above the fair weather wave base.

DESCRIPTION. Shell large, cyrtoconic, up to 18cm high and 9cm wide (Table 1) representing up to a complete volution. Coiling was exogastic and open for there is no trace of dorsal contact on fragments of any diameter. Whorl broadly depressed, ovate in transverse section, with a height to width ratio of 3:4. The smooth, broadly rounded arch of the venter and dorsum continues across the ventro- and dorsolateral areas to the rather narrowly rounded lateral areas (Figs 1-3). These are intermittently wholly taken up as the sites of large, anteriorly-facing flanged siphons, like those of *Ptenoceras*. As in *Ptenoceras* these are closed by subsequent growth which excluded detritus and thus formed so-called spines. Their detailed structure will be discussed below after shell walls. Posteriorly on the whorl the siphons are represented by small peaks instead of large spines, as previous descriptions have discussed. Dorsolaterally the walls are more depressed than ventrolaterally, they are almost flattened slopes, rather than curves, so that the dorsum can appear bluntly triangular overall. The siphuncle is near ventral, with constricted, dorsally subcyrtochoanitic necks which grade laterally into suborthochonanitic necks ventrally (Fig. 4B). The connecting rings are thick and obviously two-layered. Moderate expansion of the connecting ring within the chambers is consequent upon neck shape. A thick outer layer dorsally is developed from most of the tip of the swollen septal neck, but is more obscure in origin ventrally (Fig. 4B). This outer layer ends against the previous septum. A thin inner layer arises from the whole inner edge of the septal neck and adheres to the thick outer layer to its termination around the previous septal neck, thereafter the thin inner layer adheres to the constricted previous neck, and curved ad-posteriorly outward until it contacts the inner layer of the previous connecting ring. In this fashion the inner layers are connected to one another throughout the siphuncle's length, but the thick outer layers are localised to each chamber. Because of the curvature of the inner

TABLE 1. Morphometric data for *Diademoceras submamillatum* (Whiteaves) from the Papilio Mudstone and Burdekin Formation.

Specimen	height (mm)	W_{min} (mm)	W_{max} (mm)	Volution (°)	Node spacing (mm)
QMF11896	150	45	75	130	24,36,34
QMF32212	164	40	60	225	N/A
QMF32217	182	42	90	250	22, 28, 31, 32, 32, 34, 34
QMF32218	160	48	63	195	17, 20, 29, 24, 38, 38
QMF32219	102	40	62	135	N/A
QMF33877	125	50	64	72	35, 32
QMF33879	125	-	-	330	-
QMF33880	129	34	68	76	26

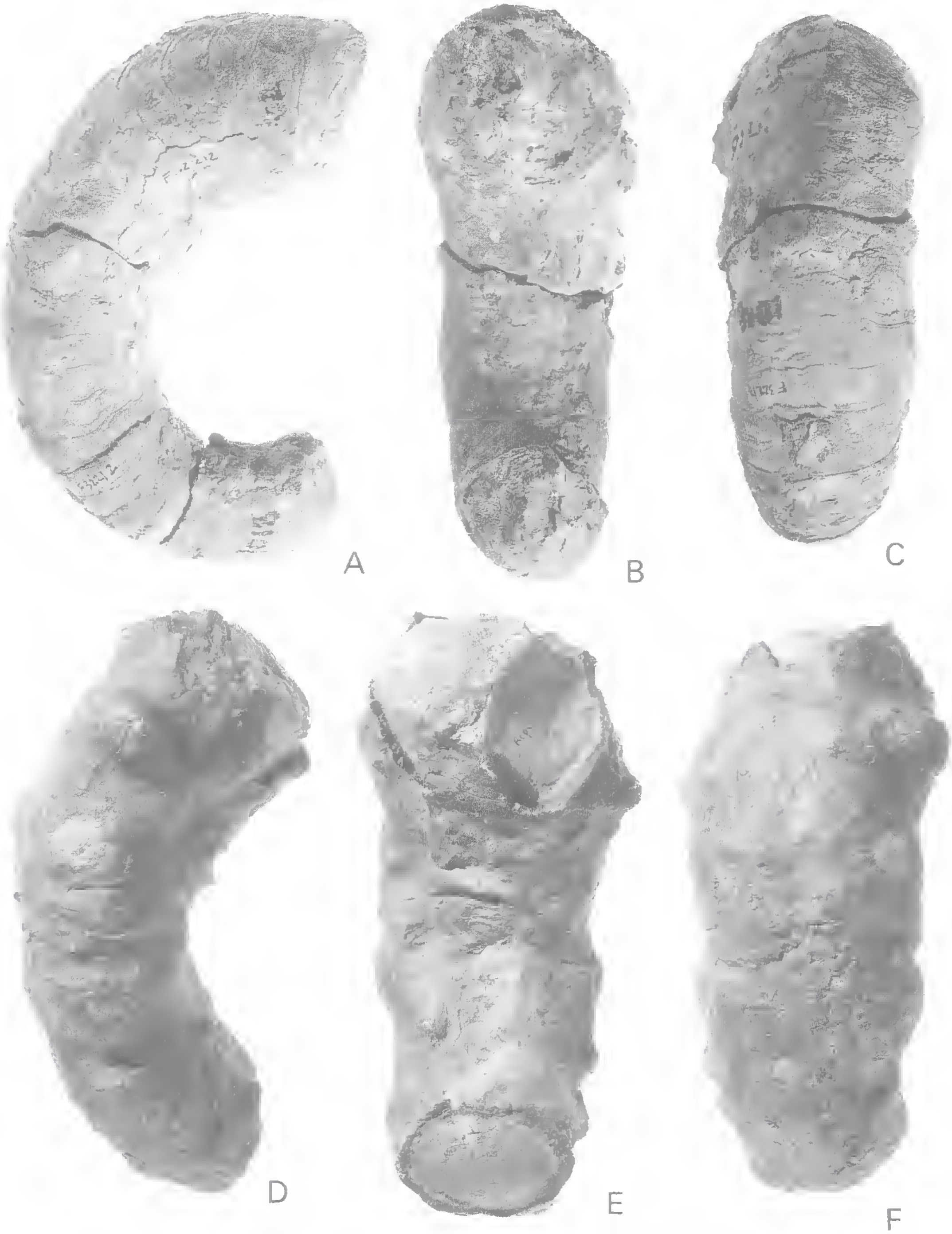

FIG. 3. *Diademoceras submammilatum* (Whiteaves) x 0.5. A-C, QMF 32212. A, side view; B,ventral view; C, dorsal view. D-F, replica of QMF11896.

layer, it did not always match the previous neck (or stay matched after death), there is often a sediment-filled space between the bent dorsum of the previous neck and the inner layer of the con-

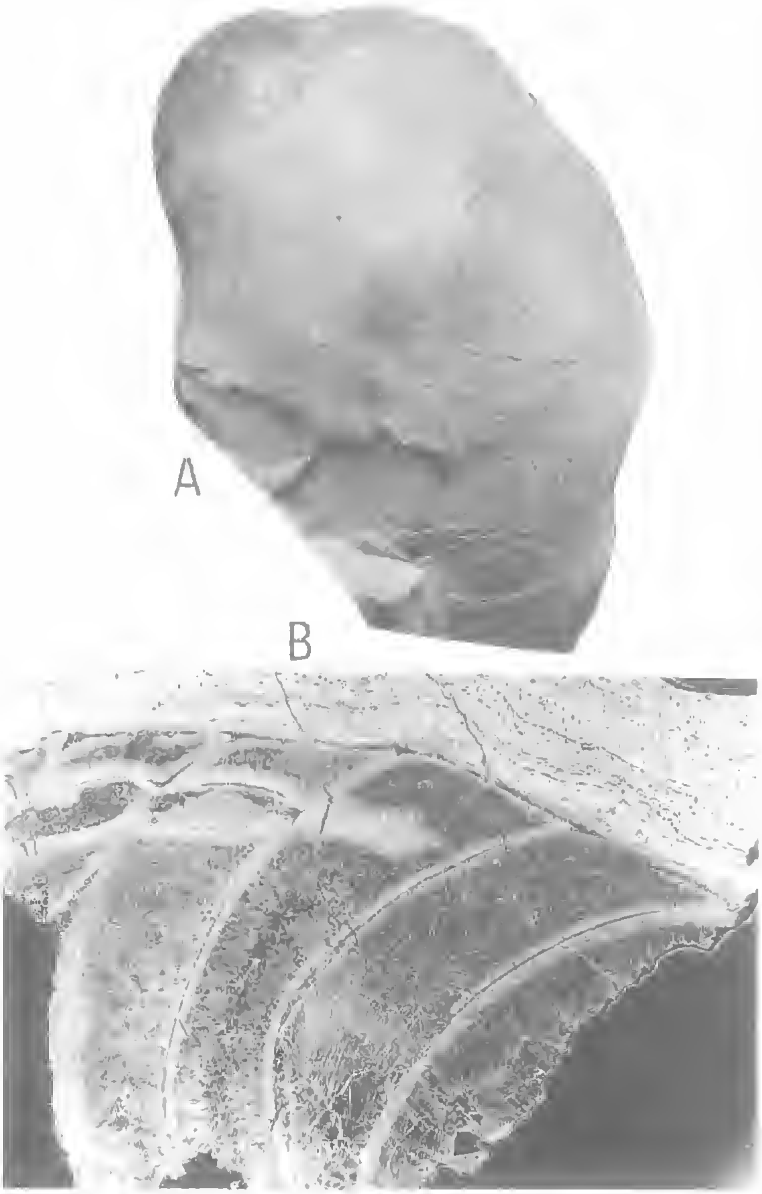

FIG. 4. *Diademoceras submammilatum* (Whiteaves), A, QMF33880, showing longitudinal ribs, faint growth lines and ventral sinus; B, Photo negative of QMF32218 slightly oblique through siphuncle, with encrusting *Clathrocoilona spissa* (Lecompte), x 1.9.

appears to be two-layered, sometimes separated by a dark line and otherwise by a gap. Poor preservation and abundance of stylolitisation within these structures does not allow us to determine with confidence whether this layering is primary or of diagenetic origin. It has the appearance of typical marine phreatic cement. The outer layer is coarsly prismatic, almost fibrous and not nearly as prone to recystallisation as the inner layer. The inner layer is thinner in smaller cross-sections, but locally varied in thickness.

External ornament, as described by Flower (1949), is poorly known on most of the specimens as five of the eight specimens are completely sheathed in encrusting stromatoporoid. QMF33880 shows strong, narrow, longitudinal ribs on the shell surface, and they are slightly reflected on the internal mould (Fig. 4A). The ribs can be detected by changes of shell thickness, in cross-sections of other specimens and also on the internal moulds of some specimens. Suture with broad, slight ventral saddle, and broad ventrolateral lobes, with narrow saddle on the sharp umbilical angle; nearly straight across the dorsum. Growth lines of QMF-33880 indicate a ventral sinus.

The shell possesses a row of short, rounded, thickly cresentic nodes oriented concave forward, relatively regularly spaced in any individual, up to 38mm apart. Sections indicate blocky calcite growth within the spines indicating they were hollow.

necting ring; this space appears in many longitudinal views of the siphuncle, and a similar space may appear more rarely ventrally.

The septa are swollen toward the dorsum of the neck and within it, but were otherwise thin. They are recrystallised wherever preserved. The septal flaps appear to have been long and relatively thick but are nowhere clearly seen. The shell wall

REMARKS. Whiteaves (1891) described a poorly preserved taxon which is of similar size, possesses similarly spaced relicts of nodes and nearly straight sutures and hence is undifferentiable from the Broken River material. The type species, *D. palmeri*, is a little smaller than Whiteaves' taxon, and has weak ventral lobes but may prove to be conspecific. *D. ventrolobatum* Lai & Zhang from the Middle Devonian of Guangxi, is significantly smaller. Wade (1988) misinterpreted the worn stromatoporoid encrusting QMF11896, the first specimen collected, intepreting this sheath as very thick layered original shell, because it faithfully reproduced the paired spines and shell outlines, and the stromatoporoid is very poorly preserved on that specimen.

If the outer wall lamina was not always present, forming symmetric lateral siphons and minor structures, and passing below every kind of epizoan, it could be suspected of being an epizoan too.

Separation of the hollow spines from the chamber by shell wall growth preceeding septa formation is observed, and validated by the shapes of exposed chamber fills which show the smooth, low rises under the nodes. Only the clean node-fills witness to front walls to the nodes, and the calcite growth, interpreted as phreatic growth, testifies to their shape as do the epizoan overgrowths. The smooth shell wall bases were perhaps added to the living chamber soon after the shell's siphons were closed, by reactivation of the mantle. All cephalopods repair by mantle reactivation, so this method is not unusual, and the gradual forward movement of the growing body would bring a smooth curve of body adjacent to the space within the closed siphon. This would allow a slight bulge, and account for the observed shape of the walls.

The undoubtably aragonitic nautiloid shell recrystallised so completely, an explanation of the relatively good preservation of the microstructure of the stromatoporoid is required. Such differential preservation in these specimens would suggest that the original stromatoporoid mineralogy differed from that of the nautiloid, and by inference was probably calcitic. Stromatoporoids have been variously inferred as having skeletons which were calcitic (Galloway, 1957; Kershaw, 1990; Rush & Chafetz, 1991) or aragonitic (Stearn, 1975; Stearn & Mah, 1987). This material shows circumstantial evidence that the stromatoporoid was calcitic, but demonstrates no more than association of preserved calcite phases than Kershaw (1990).

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